Development of *Eucelatoria bryani* and *Eucelatoria rubentis* (Diptera: Tachinidae) in Different Instars of *Helicoverpa zea* (Lepidoptera: Noctuidae)

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ABSTRACT Development of the tachinids *Eucelatoria bryani* Sabrosky and *E. rubentis* (Coquillett) in the last 2 larval instars of the host corn earworm, *Helicoverpa zea* (Boddie), was examined. Developmental differences exist between parasitoid species, and within a species, depending on host instar at the time of parasitization. Development was fastest for *E. bryani* reared in hosts parasitized as 5th instars and was slowest for *E. rubentis* reared from hosts parasitized as 4th instars. These 2 closely related species also differ in their physiological relationship with *H. zea*. Second and 3rd instars of *E. rubentis* become enclosed in a thickened gelatinous sheath, probably of host origin. Such a sheath does not form around larvae of *E. bryani*. Size of *E. bryani* was not affected by host instar at the time of parasitization. Host instar at the time of parasitization did not affect the size of *E. rubentis* females, but *E. rubentis* males were significantly larger from hosts parasitized as 5th instars. Although both species deposited larger clutches of eggs in older hosts, clutch size was greater in both host-instars for *E. bryani* than for *E. rubentis*. Its greater clutch size and lack of size variation in its progeny reared from different host classes indicate that *E. bryani* is more efficient in using *H. zea* as a host resource. Given its faster larval development, *E. bryani* should be a superior larval competitor when both species parasitize *H. zea*. Interspecific differences may result from *E. bryani* being more of a specialist parasitoid whereas *E. rubentis* is more polyphagous.

KEY WORDS *Eucelatoria, Helicoverpa zea,* host–parasitoid relationship, parasitoid development, koinobiont

HOST SIZE AND developmental stage at the time of parasitization can affect life history traits of parasitoid progeny. For koinobiont parasitoids, where hosts continue to feed and grow during at least some part of parasitoid development (Askew and Shaw 1986), parasitization of different host instars can affect progeny development time (Weseloh 1984, Nechols and Kikuchi 1985, Löhr et al. 1989, Petitt and Wietlisbach 1993) and size (Strand et al. 1988, Sequeira and Mackauer 1992). The latter aspect is particularly important because parasitoid size is often positively correlated with female fecundity (Elsey and Rabb 1970, King et al. 1976, Opp and Luck 1986, Harvey et al. 1994, Reitz and Adler 1995).

Members of the genus *Eucelatoria* Townsend are facultatively gregarious endoparasitoids of a variety of larval noctuids (Lepidoptera) (Arnaud 1978, Sabrosky 1981). They are koinobionts, and hosts that are parasitized before the ultimate instar molt at least once (Reitz and Nettles 1994). *Eucelatoria bryani* Sabrosky is an oligophagous parasitoid whose host range appears restricted to the *Helicoverpa/Heliothis* species complex (Jackson et al. 1969, Sabrosky 1981; S.R.R., unpublished data). *E. bryani* can parasitize a wide range of corn earworm, *Helicoverpa zea* (Boddie), larval stages from 2nd instars to prepupal 5th instars, with 4th instars and feeding-stage 5th instars being the more favored stages (Martin et al. 1989). *Eucelatoria rubentis* (Coquillett) can parasitize a similar range of *H. zea* developmental stages as *E. bryani* (Reitz 1994). However, *E. rubentis* is a much more polyphagous parasitoid than *E. bryani*, having been reared from at least 12 genera of Noctuidae (Arnaud 1978, Sabrosky 1981; S.R.R., unpublished data).

The purpose of this study was to examine developmental differences between *E. bryani* and *E. rubentis* when parasitizing 4th and 5th instars of the host *H. zea*, and relate how interspecific differences in development might affect the intrinsic competitive abilities of these 2 species. Although host instar at the time of parasitization affects the development time of *E. bryani* in *Helicoverpa armigera* (Hübner) (Mani and Nagarkatti 1981), at what point these differences occur, and if interspecific differences between *E. bryani* and *E. rubentis* exist, are unknown. Specifically, I determined if

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developmental rates differ between *E. bryani* and *E. rubentis* and between members of the same species from hosts parasitized as 4th or 5th instars, at what stages of host and parasitoid development differences occur, and if host instar affects the size of adult *E. bryani* and *E. rubentis*.

Materials and Methods

All experiments were conducted in a walk-in environmental chamber maintained at 27 ± 2°C, 65 ± 10% RH, and a photoperiod of 14:10 (L:D) h. *H. zea* larvae were maintained in individual plastic cups (30 ml) filled halfway with artificial wheat germ-pinto bean media (Burton 1969, as modified in Adler and Adler 1988). *E. bryani* and *E. rubentis* adults were reared in Plexiglas cages (40 by 40 by 40 cm) containing 100–200 adult flies per cage. Flies were provided with damp sponges and sugar (sucrose) cubes. For colony maintenance, flies were repeatedly provided with groups of ≈20 *H. zea* 5th instars. Each group of larvae was placed in a cage for 30–60 min to ensure parasitism.

There were 4 separate treatment groups for this study: 4th and 5th instars of *H. zea* parasitized by *E. bryani*, and 4th and 5th instars of *H. zea* parasitized by *E. rubentis*. Day 1 fourth, and day 1 fifth instars of *H. zea* were used for all experiments. These larvae were obtained by selecting premolting 3rd and 4th instars of *H. zea*, on the basis of head capsule slippage (Neunzig 1969), the afternoon (9 h after lights on) before they were to be parasitized. Only larvae that had molted by the next morning were used.

Each larva was exposed to an individual female parasitoid which was allowed to oviposit only once. All parasitizations were done between 2 and 4 h after lights on. Host larvae were weighed within 1 h before parasitism.

Groups of *H. zea* larvae (n = 12 per treatment group) were dissected immediately following parasitism (0 h), and every 12 h thereafter for 108 h, for a total of 10 time intervals. At each time interval, developmental stages of the *H. zea* larvae were determined, according to the stages of Webb and Dahlman (1985). Upon dissection, the development stage and location within the host of each parasitoid immature were recorded. The 3 larval instars of *E.* spp. can be separated on the basis of the size and structure of the cephalopharyngeal apparatus and posterior spiracles (Ziser and Nettles 1978; S.R.R., unpublished data). The length and width of each immature parasitoid, along its dorsal surface, was measured with a stereomicroscope fitted with an ocular micrometer. The product of length × width measures was used as a measure of overall body size.

Additional groups (n = 25 per group) of *H. zea* larvae were parasitized and held until adult parasitoid eclosion, to determine the length of *E. bryani* and *E. rubentis* larval and pupal stages. These groups (hereafter referred to as the control groups) were inspected every 6 h until the parasitoids pupariated, and then for adult emergence. Nine days after parasitization, puparia were weighed to the nearest 0.1 mg (wet mass) and their size (length × width) measured. After adult eclosion, the metathoracic tibia of each individual was measured, because tibial length is correlated with body weight (Reitz and Alder 1995).

To determine if development and growth rates differed between parasitoid species, and within species developing in different host instars, two analyses were necessary. In the 1st, the frequency distributions of immature stages of *Eucelatoria* among the 4 treatment groups at each time interval were compared using a log-linear model (PROC CATMOD, SAS Institute 1985). Secondly, even if the distributions of immature stages did not differ, growth rates, as reflected by body size, could still differ across species and host instars. Therefore, the sizes of parasitoids at each time interval relative to their respective mean puparial size were compared. These proportions of maggot size to mean puparial size, were regressed over time, and the homogeneity of the 4 slopes was tested (PROC GLM, SAS Institute 1985).

Using the control groups, the durations of larval and pupal stages, and total times until adult eclosion among the 4 treatment groups were compared using analysis of variance. Because *E.* spp. are protandrous, data were analyzed separately for males and females. Therefore, response variables were the mean time periods for all members of a sex within a clutch. Independent variables in the models were parasitoid species and *H. zea* instar at the time of parasitism. Data for progeny size were analyzed in a similar manner. The response variables here were the mean puparial weight, size, and tibial length for all members of a sex within a clutch. Where appropriate, analyses are based on log-transformed values. Means separations are based on least-squares means t-tests (LSMeans option of PROC GLM, SAS Institute 1985).

Results

Mean clutch size for *E. bryani* was significantly greater than that for *E. rubentis* (F = 9.06; df = 1, 92; P = 0.003; Table 1). Mean clutch size was significantly greater for both *E. bryani* and *E. rubentis* when females oviposited in 5th-instar hosts than 4th-instar hosts (F = 11.42; df = 1, 92; P = 0.001). However, differences in clutch sizes were consistent between the 2 parasitoid species for the 2 host instars (F = 0.05; df = 1, 92; P > 0.80, for species × host-instar interaction).

Eucelatoria spp. oviposit just under the cuticle, in the muscle wall of the host, and development begins soon after oviposition. Larval development and growth were more rapid for *E. bryani* than *E. rubentis* (Figs. 1 and 2). Both *E. bryani* and *E. rubentis* larvae developed faster in *H. zea* parasitized as 5th instars than in those parasitized as 4th

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E. bryani	5th
E. rubentis	4th
E. rubentis	5th

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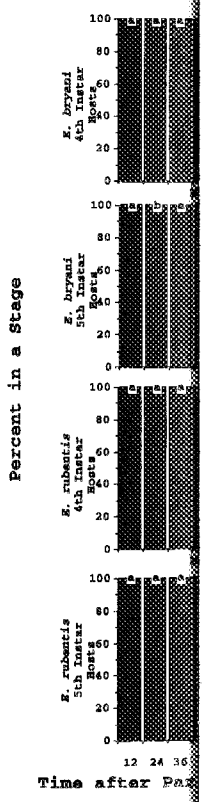

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Table 1. Clutch size (mean ± SE, eggs per host), and development times (mean ± SE, in days) of *E. bryani* and *E. rubentis* from *H. zea* hosts parasitized as 4th and 5th instars

Species	Host instar	Clutch size	Female total development time	Male total development time	Female larval time	Male larval time	Female pupal time	Male pupal time
E. bryani	4th	2.38 ± 0.26ab	11.6 ± 0.16a	11.1 ± 0.23a	4.0 ± 0.12a	3.9 ± 0.21a	7.6 ± 0.16a	7.2 ± 0.14a
E. bryani	5th	3.61 ± 0.48c	11.2 ± 0.11b	10.7 ± 0.15a	3.5 ± 0.08b	3.4 ± 0.09b	7.7 ± 0.10a	7.3 ± 0.13a
E. rubentis	4th	1.48 ± 0.15a	12.4 ± 0.34c	12.1 ± 0.26b	4.6 ± 0.29c	4.7 ± 0.23c	7.8 ± 0.16a	7.4 ± 0.13a
E. rubentis	5th	2.50 ± 0.28b	12.2 ± 0.11c	12.0 ± 0.11b	4.1 ± 0.08a	4.1 ± 0.11a	8.1 ± 0.08b	7.9 ± 0.11b

Means in a column followed by the same letter are not significantly different ($P > 0.05$; least-squares means t-test).

instars. Growth rates of the parasitoid maggots in the 4 treatment groups reflect these differences in larval development (F = 9.69; df = 3, 346; $P < 0.0001$, test for homogeneity of slopes for growth rates; Fig. 2). The fastest growing larvae of the 4 treatment groups were *E. bryani* in hosts parasitized as 5th instars (slope ± SE = 0.0258 ± 0.0010, for log-transformed data), whereas the slowest growing larvae were *E. rubentis* in hosts parasitized as 4th instars (slope = 0.0202 ± 0.0010). The growth rates for *E. bryani* in hosts parasitized as 4th instars (slope = 0.0230 ± 0.0010) and *E. rubentis* in hosts parasitized as 5th instars (slope = 0.0237 ± 0.0007) were intermediate in growth rate and did not differ significantly from one another (t = 0.68, P = 0.50).

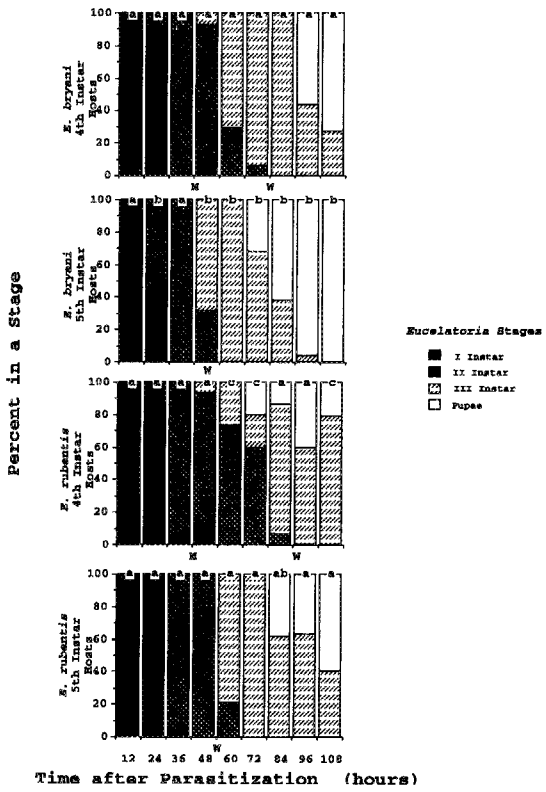

Fig. 1. Distribution of immature stages (I, II, III instars, and pupae) of *E. bryani* and *E. rubentis* at 12-h intervals following parasitism of 4th and 5th instars of *H. zea*. For each time interval (across graphs), bars marked with the same letter indicate stage distributions that are not significantly different ($P > 0.05$, log-linear models). Median times for 4th instars of *H. zea* molting to 5th instars (M), and initiation of the wandering phase of 5th instars (W) are marked on the time axis for each treatment group.

Twelve hours after oviposition all maggots were 1st instars. At 12 h most maggots were still located in the muscle wall of the host (67 and 65% for *E. bryani* and *E. rubentis*, respectively, in 4th-instar hosts, and 86% for *E. rubentis* in 5th-instar hosts), but the majority (87%) of *E. bryani* in 5th-instar hosts had already crossed into the hemocoel of the host. First-instar maggots did not attach to host tracheae until late in the stadium and appeared to remain hematophagous. At 24 h after parasitism, 60% of *E. bryani* in 5th-instar hosts had molted to 2nd instars, whereas only one *E. bryani* from a 4th-instar host had molted to the 2nd instar and no *E. rubentis* had molted to the 2nd instar (Fig. 1).

At 36 h, almost all larvae in the 4 treatment groups were 2nd instars (Fig. 1), but *E. bryani* from *H. zea* parasitized as 5th instars were larger (relative to puparial size) than maggots from the other 3 groups (Fig. 2). Second instars of both parasitoid species established respiratory attachments to host tracheae. Typically, these attachments were made to a lateral tracheal trunk near a spiracle. During the 2nd stadium, melanized, spongy gelatinous sheathes formed around *E. rubentis* larvae. Also, the *H. zea* tracheae in the vicinity of *E. rubentis* respiratory attachments became melanized. No such thickened, spongy melanized sheathes formed around *E. bryani* larvae. Five *E. bryani* larvae (1%) did appear to be partially enclosed in a thinner filmlike sheath, but no melanization appeared in the tracheae of any *H. zea* parasitized by *E. bryani*. At 36 h after parasitism, most of *H. zea* parasitized as 4th instars had molted to the 5th instar.

The next major difference in development occurred at 48 h, where most (69%) of the *E. bryani* in 5th-instar hosts were 3rd instars, whereas most of the maggots in the other 3 groups were still 2nd instars (Fig. 1). Third-instar maggots also formed respiratory attachments to major tracheae in the host. As with 2nd instars, 3rd instars of *E. rubentis* were surrounded by a spongy, melanized sheath, and host tracheae were melanized in the vicinity of the parasitoid respiratory attachment. These

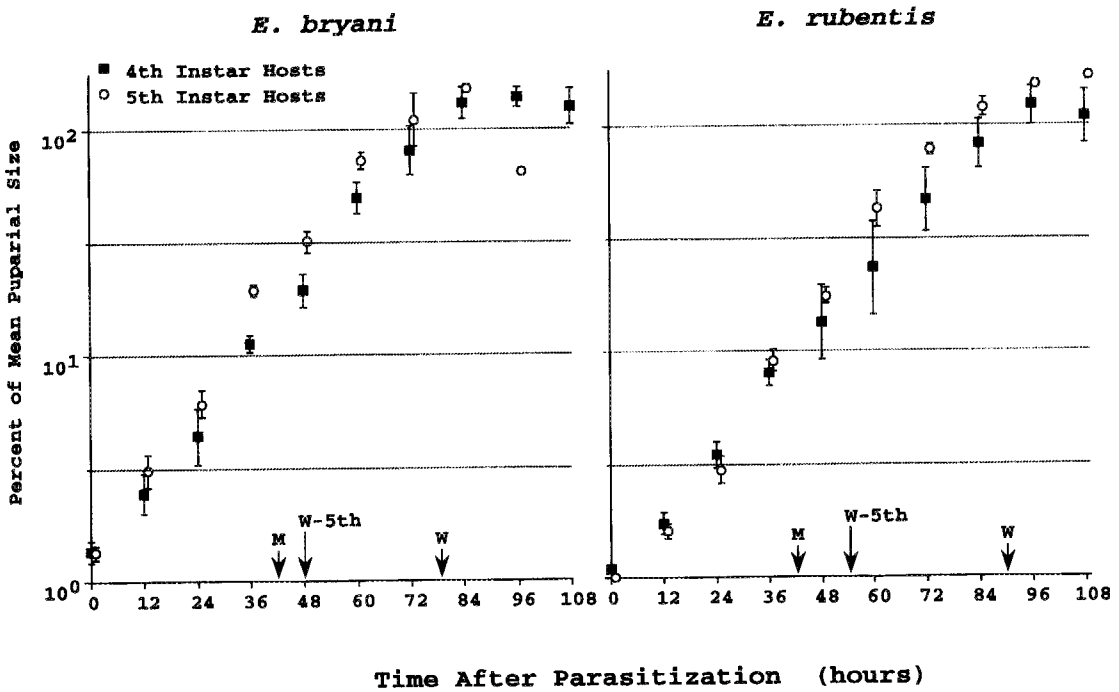

Fig. 2. Growth rates of *E. bryani* and *E. rubentis* at 12-h intervals following parasitism of 4th and 5th instars of *H. zea*. Mean larval sizes (length × width) relative to mean puparial size (length × width) for each treatment group are plotted for each time interval. Bars represent 95% CL. Median times for 4th instars of *H. zea* molting to 5th instars (M) and initiating their wandering phase as 5th instars (W), and for initiation of wandering phase of *H. zea* parasitized as 5th instars (W-5th) are marked on the time axis.

sheathes appeared thicker around 3rd instars compared with sheathes surrounding 2nd instars. Again, no such sheathes formed around *E. bryani* larvae, nor did the tracheae of larvae parasitized by *E. bryani* show melanization. Between 48 and 60 h after parasitism, most hosts parasitized as 5th instars had initiated their wandering phase. Hosts parasitized as 4th instars began wandering between 72 and 84 h after parasitism. For both stages, *H. zea* parasitized by *E. rubentis* initiated this final wandering phase later than those parasitized by *E. bryani*. After host death, 3rd-instars of both parasitoid species detached from their respiratory attachments and began scavenging in the host carcass. At this point, *E. rubentis* larvae extricated themselves from their surrounding sheath.

The 1st *E. bryani* and *E. rubentis* puparia formed between 60 and 72 h after parasitism, from 1 *H. zea* parasitized as a 5th instar and 1 *H. zea* parasitized as a 4th instar, respectively. These 1st *E. rubentis* puparia (n = 3) emerged from a host that died before molting to the 5th instar, and the puparia were considerably smaller (mean ± SD = 9.59 ± 4.71 mm^2) than those in the control group (16.34 ± 5.01 mm^2).

Puparia had formed from hosts in all 4 treatment groups by 96 h after parasitism. Again, *E. bryani* from hosts parasitized as 5th instars developed the fastest, as evidenced by the higher frequency of puparia compared with the 3 other groups (Fig. 1). Only 1 maggot from that group had not pupariated by this time. At 108 h, all *E. bryani* from hosts parasitized as 5th instars had pupariated, whereas only 73% of *E. bryani* from hosts parasitized as 4th instars, 60% of *E. rubentis* from 5th instars, and 21% of *E. rubentis* from 4th instars had pupariated.

Total development (combined larval and pupal time) was faster for *E. bryani* than *E. rubentis* (F = 34.4; df = 1, 67; $P < 0.0001$, for females; F = 47.9; df = 1, 57; $P < 0.0001$; for males; Table 1). Among females of both species, total development time was shortest for *E. bryani* from hosts parasitized as 5th instars (Table 1). These females also had the shortest mean larval period, but their mean pupal period was not significantly shorter than those of *E. bryani* and *E. rubentis* females from hosts parasitized as 4th instars. Although *E. rubentis* females from hosts parasitized as 5th instars had a significantly shorter mean larval period than those from hosts parasitized as 4th instars, their mean pupal period was significantly longer. Hence, there was no difference in total development time for *E. rubentis* females in 4th- or 5th-instar hosts.

Development times for males showed a pattern similar to that of females, with the only exception being the lack of a significant difference in total development time between the 2 *E. bryani* groups (Table 1). Although the larval stage was shorter for

Table 2. Progeny size (mean ± SE) of *E. bryani* and *E. rubentis* from *H. zea* hosts parasitized as 4th and 5th instars

Species	Host instar	Female puparial size, mm^2 [a]	Male puparial size, mm^2	Female puparial wt, mg	Male puparial wt, mg	Female tibial length, mm	Male tibial length, mm
E. bryani	4th	16.34 ± 0.80a	16.98 ± 0.46a	23.38 ± 1.58a	24.37 ± 1.07a	1.83 ± 0.04a	1.99 ± 0.03ab
E. bryani	5th	16.71 ± 0.45a	16.74 ± 0.51a	24.05 ± 0.96a	23.90 ± 0.96a	1.85 ± 0.26a	1.95 ± 0.03ab
E. rubentis	4th	16.39 ± 1.07a	16.29 ± 1.30a	22.88 ± 2.13a	22.99 ± 2.49a	1.78 ± 0.05a	1.88 ± 0.09a
E. rubentis	5th	17.74 ± 0.94a	20.41 ± 0.62b	25.62 ± 1.82a	31.10 ± 1.34b	1.84 ± 0.90a	2.06 ± 0.04b

Means in a column followed by the same letter are not significantly different ($P > 0.05$; least-squares means t-test).
[a] Puparial size equals length × width, measured along the dorsal surface.

E. bryani from hosts parasitized as 5th instars, there was no significant difference between the length of the pupal period for *E. bryani* from hosts parasitized as 4th or 5th instars. As with *E. bryani* males, the larval period was significantly shorter for *E. rubentis* males from hosts parasitized as 5th instars than from hosts parasitized as 4th instars, but the trend for the pupal periods was in the opposite direction, with pupal period being significantly shorter for *E. rubentis* males from hosts parasitized as 4th instars.

There were no significant differences in the size of either female or male *E. bryani* progeny reared from hosts parasitized as 4th instars or those parasitized as 5th instars (Table 2). In contrast to *E. bryani*, *E. rubentis* male progeny from 5th-instar hosts were significantly larger than male progeny from 4th-instar hosts (Table 2). However, *E. rubentis* females reared from hosts parasitized as 4th instars and those parasitized as 5th instars were not significantly different in size (Table 2).

Discussion

Although there are similarities in development of *E. bryani* and *E. rubentis* in *H. zea*, striking interspecific differences in the host–parasitoid relationship exist between *E. bryani* and *E. rubentis*. Larval development of both species is continuous, commencing upon oviposition. Although slower in younger hosts, there is no cessation of parasitoid development related to discrete events in host development (Mellini 1990), as occurs with other species of Tachinidae (Schoonhoven 1962, Shields 1976, Baronio and Sehnal 1980, Ramadhane et al. 1987, Bratti et al. 1992). In 4th-instar hosts, almost all larvae of *E. bryani* and *E. rubentis* had molted to the 2nd instar before the hosts had molted to their final (5th) instar. Also, *E. bryani* and *E. rubentis* larvae molted to the 3rd instar both before and after their hosts began their final wandering phase. Interestingly, parasitism induces precocious wandering (Reitz and Nettles 1994), but this precocious wandering occurs earlier in *H. zea* parasitized by *E. bryani* than *E. rubentis*.

Development of *E.* spp. may be partially dependent on host ontogeny. *H. zea* also cease feeding, and wander in preparation for ecdysis before molting from the 4th to the 5th instar, (Adler and Adler 1988). Therefore, with hosts not feeding, less food might be available for parasitoids resulting in their slower development (Smilowitz and Iwantsch 1973). Alternatively, slower development in younger hosts may be an active response by parasitoid larvae to mitigate damage to the host until the host is large enough to support the parasitoids adequately (Slansky 1986). Weseloh (1984) has also suggested that *Compsilura concinnata* (Meigen) develops slower in younger hosts because of higher juvenile hormone levels in younger hosts relative to older hosts, and not because of less abundant food supplies. Although this scenario is possible for *E.* spp., juvenile hormone analogs, applied topically to *H. armigera* or *H. zea*, only inhibit adult eclosion and not larval development or pupariation of *E. bryani* (Divikar 1980; S.R.R., unpublished data).

Although larval periods for both parasitoid species were longer when parasitizing 4th-instar hosts, their pupal periods did not show a similar, consistent relationship between the species. Pupariation occurs throughout the day, but adult eclosion only occurs in the morning. Therefore, *E. rubentis* from hosts parasitized as 4th instars may reach a suitable level of development for adult eclosion 1 gate (Beck 1980) earlier than those from hosts parasitized as 5th instars.

One of the most notable differences between *E. bryani* and *E. rubentis* when they parasitize *H. zea* is the sheath that forms around larvae of *E. rubentis* but does not form around larvae of *E. bryani*. Because the sheath virtually encloses a maggot as an amorphous sac, this sheath appears to be an immune response by the host to the presence of *E. rubentis* rather than a well-defined respiratory funnel that occurs in other tachinid parasitoid-host associations (Clausen 1962, Ferrar 1987, Mellini 1990). The extensive nature of the sheath may hinder foraging by *E. rubentis* larvae, partially accounting for their slower rate of development compared with *E. bryani*. *E. bryani* larvae do not elicit this response even though they also attach to host tracheae. Interestingly, an extensive respiratory funnel is reported to form when *E. bryani* parasitizes *H. virescens* (Ziser and Nettles 1978). There is a precedent for differential host immune responses by *H. zea* and *H. virescens* to the same parasitoid species. *Cardiochiles nigriceps* Viereck eggs are encapsulated by *H. zea* but resist encapsulation by *H. virescens* (Lewis and Vinson 1968).

Strand (1986) has suggested that specialist and generalist parasitoids will elicit different host immune responses in the same host species. The differences between *E. bryani* and *E. rubentis* suggest that *E. bryani* is more closely associated with *H. zea* and has evolved mechanisms for suppressing *H. zea* immune responses that trigger the formation of the sheath, whereas such host-specific mechanisms are lacking in the more polyphagous *E. rubentis*. Still, the presence of this sheath does not adversely affect the survival of *E. rubentis*.

Size and development rate are 2 life history traits that parasitoids must balance according to host quality. Gregarious parasitoids, such as *E. bryani* and *E. rubentis*, can further influence this relationship by adjusting clutch size in response to host quality (Gross and Rogers 1995, Reitz and Adler 1995). *E. bryani* parasitize older hosts more heavily, but progeny size does not vary with host age or size. *E. rubentis* also varies clutch size in response to host quality; however, the relationship between parasitoid size and development time differs from that of *E. bryani*. Although there was no significant difference in total development time, *E. rubentis* males from older *H. zea* were considerably larger (>35%, by weight) than those from younger hosts. This size variation with host instar did not occur among *E. rubentis* females. Because *E. rubentis* males are larger than females, and larger than *E. bryani*, younger hosts may not attain a sufficient size to produce males as large as those from older hosts. These facts, combined with the result that *E. bryani* always had significantly larger clutch sizes, indicate that the suitability of different *H. zea* instars varies interspecifically and may reflect the host specialization of *E. bryani* and relative polyphagy of *E. rubentis*. Despite these differences, both species can develop successfully in different instars of *H. zea*. This plasticity in host suitability allows female parasitoids to gain in fitness even when the most suitable host stages are not available (Charnov and Skinner 1985) and would be especially important considering the variable phenology of host populations (Fitt 1989, Raulston et al. 1990, Steward et al. 1990, Archer and Bynum 1994) and consequent probability of females encountering a range of host stages.

Practically, differences in host–parasitoid relationships among parasitoid species have ecological consequences and implications for biological control (Doutt et al. 1976, Luck and Podoler 1985, Opp and Luck 1986). For example, *E. bryani* produces larger clutches than *E. rubentis*. Also, because of its faster larval development, *E. bryani* should be a superior larval competitor compared with *E. rubentis* when parasitizing *H. zea*. These factors should be considered in assessing these species, and other species, as biological control agents of *H. zea*.

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